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Introduction

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Weir sex: the underappreciated diversity of sexual reproduction

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The idea for this project started over lunch in an Italian restaurant in Copenhagen in 2010. We were not planning to talk about sex at that time, but to discuss the evolution of uniparental inheritance. But as they say, one thing leads to another, and we started to talk about sex and its underappreciated weirdness. And the need for a project like this. Along the way, we were continuously reminded of the importance of such a project: the most recent example was a comment in an undergraduate 'learning diary', a teaching tool in which students are asked to explain hard to understand concepts, or concepts that are surprising to them. The student expressed great surprise to hear that vertebrate sex determination does not always follow the 'normal' XY pattern; in birds, sex is instead determined by ZW chromosomes and females are the heterogametic sex. Well, we thought, if ZW sex determination seems 'weird', then you ain't seen nothing yet!

The student of course was not stupid, merely rather uninformed—or better put: biased in the same way we all tend to begin our careers as biologists. Our academic forays in sex and sexual selection start by learning that there are primary and secondary sexual characteristics, that these differences are caused by sex chromosomes, packaged in different kinds of gametes that need to come together by one type of gamete (sperm) finding the other (egg) via mostly internal fertilization. Only later might we realize that sex determination mechanisms are so diverse they deserve an entire book [1]. If we then retain our interest, at some point we learn, to our surprise, that monogamy is a really unusual reproductive system, and that sex itself isn't a self-evident feature of all reproduction. Even more so, sexual reproduction is a *contradictio in terminis*, since sex, in its very essence, involves fusion of gametes, thus *reducing* numbers instead of *increasing* numbers. The very existence and persistence of sexual reproduction remains an evolutionary puzzle.

The list goes on. Selfing is common in plants, while more than a few animals also appear to have no objection to self-fertilization. Similarly, most evolutionary biologists are surprised when they learn that hermaphroditism in animals is actually rather widespread: close to 30% of all species are hermaphrodites [2]. Most plants do not have separate sexes, while the notion of 'maleness' and 'femaleness' becomes something rather different when one includes fungi and unicellular life. Slowly then, as we learn more, our minds open up.

One could argue that whatever field one chooses, biology is so diverse that it is impossible to expose students to the entire bewildering array of biological phenomena; let us then at least try to understand the best-studied model systems and hope that they are in some sense representative examples of what goes on in nature. Fair point. But when it comes to sex at least, it is easy to become intrigued by its wonderful diversity. Why, then, do we still so narrow-mindedly stick to the familiar?

In psychology, WEIRD is an acronym for 'Western, educated, industrialized, rich and democratic'—referring to the most widely used subject that psychology researchers have access to, and whose behaviour might be interesting but not particularly representative of human behaviour across cultures. Hence, using *Weir* in the title of our issue seems rather appropriate, albeit

with an obvious twist. If you have been paying attention so far, you might rightfully ask why we decided to give this special issue the title *Weird Sex* if the actual argument we want to make is that it is the conventional organisms we tend to study that are the odd ones out? Our obsession with studying what is most familiar to us equates to a study of phenomena that might actually be rather unusual. We may miss out on many fascinating questions in evolution if we don't remove our biases, while building 'general' theories that only apply if a narrow set of assumptions are met. Hence, *Weird Sex* really refers to our weird tendency to ignore most of what lives around us.

Once we have abandoned our implicit and explicit assumptions regarding how sex 'ought' to occur, we start to realize that there are many questions to be asked. Sex in the classical sense is not the only way to swap genes [3], so why do so many organisms insist on a complex cocktail of the four features of meiotic sex [4]? Sex is very often facultative rather than obligate, yet the organisms most familiar to us are mostly obligatorily sexual [5]. Why is that? Despite our focus on sexual dimorphism, sex doesn't have to involve males and females; therefore, why are there so often precisely two mating types even in systems that lack male–female asymmetry [6]? The list goes on.

A first hurdle to overcome by anyone willing to start asking the kind of questions we alluded to above is taxon-specific terminology. Because textbooks tend to use well-known examples (peacocks, humans, *Drosophila*, etc.) to introduce the fascinating and often conflicting selection pressures related to sex, we are mainly acquainted with terms such as sperm, egg, mitosis, meiosis and recombination. (Interestingly, the recently published Princeton Guide to Evolution [7] lists no fewer than six different definitions for recombination, varying in the range of phenomena that are included; clearly, even supposedly stock-standard terms feature quite some diversity.) Specialist terminology is often necessary to precisely describe non-conventional organisms and behaviours, and as an unfortunate consequence, papers brimming with unfamiliar terminology are not easily seen as relevant to the study of sex, sexual selection or sexual conflict, in general. Try explaining how a female can mate with her male offspring whose dad was the male offspring of the male's mate [8]. At the same time, researchers sometimes use the same terminology but mean fundamentally different things. 'Male' and 'female' as used in fungal sex are fundamentally different beasts than conventional males and females [9,10].

We deliberately did not impose any terminology or concepts on our authors, for trying to do so might backfire. In some sense, it would be clearest if 'male' and 'female' were only talked about when there is a size difference between two types of gametes, but the terms are sometimes also used to include 'those that actively seek a mate' as males (e.g. a definition based on motility) [11]. Accepting this means that 'why do males more often actively seek mates?' is a tautological consequence of a definition in one field while it can be a genuine research avenue in another. This is a somewhat awkward state of affairs, but our pragmatic approach is to accept that seeking analogies can help. Features such as the 'male-biased' operational sex ratio of a population of monokaryons and dikaryons [7,10] can truly help link findings in studies on fungi to existing theory, even if that theory is based on the sex life of a multicellular gonochorist animal. Moreover, it would probably be parochial of us to reserve succinct

terminology to be used only in contexts that are most familiar to us. Such 'demand' would probably backfire, if the quest is to remind people that analogous ideas can be repeated, with fascinating differences, across life. Thus, pragmatically, we have let authors use their preferred terminology, ignoring definitional debates. In a sense, the very existence of such 'grey zones' again highlights the immense diversity of life: there's more diversity out there than we often remember, and some properties of sexual (and asexual) lifecycles are shared among many systems, while others are refreshingly different once we dare to look.

The topics addressed in this special issue range from very fundamental questions such as the evolutionary benefits [12] and the origin of sex [3,4,13] and mating types [6], to secondary consequences of sexual reproduction, such as sexual selection [5,11] and the increased scope for genetic conflict [8,10,14], and the cost of sex, either due to the production of males in anisogamous species or due to mate finding or mechanisms of meiosis [15].

While sexual reproduction in most organisms involves a syndrome of various characteristics (gamete fusion, nuclear fusion leading to ploidy change and meiosis), Vreeburg *et al.* [10] describe that in basidiomycete fungi gamete fusion and genomic amalgamation usually are separated in time. This begs for a definition of sex that catches its very essence. Is it the essence of sex gamete fusion? Is it nuclear mixing? Or is it meiosis? According to Vreeburg *et al.* [10], sex is 'the union of two haploid nuclei, each produced by meiosis, in due course followed by a reduction of the genome through meiosis', a slightly modified version of Dick's [16] definition. Genetic mixing and meiosis are thus crucial components of eukaryotic sex. Therefore, Lenormand *et al.* [13] start this issue with a review of the evolution of one of the hallmarks of sex, meiosis. However, as pointed out by Speijer [4], for each of the four separate but interlocking mechanisms of complete meiotic sex, prokaryotic factors and/or processes can be identified as evolutionary predecessors. Therefore, Ambur *et al.* [3] discuss the prokaryotic way of mixing of genetic material via transformation, which does not involve meiosis.

But what are the evolutionary benefits of sex? Ambur *et al.* [3] conclude that bacterial transformation most likely facilitates genomic conservation, rather than genomic innovation. Pesce *et al.* [12] briefly review the existing hypotheses for the benefits of sex, and focus on recent *in vitro* experiments, 'sex in a test tube', to test those hypotheses. Tilquin & Kokko [17] attempt to make sense of the geographical distribution of sex and asex. Whatever be the exact definition of sex, the biological entities that are to fuse (usually gametes) must find each other first. Therefore, Hadjivasiliou & Pomiankowski [6] discuss a neglected hypothesis that there is a need for asymmetric signalling interactions between cells—that are to become mating partners—for efficient localization, which is a novel hypothesis for the evolutionary origin of mating types [18].

After discussing the above fundamental questions, the next series of papers focuses on secondary consequences of sex. We are used to thinking of sex in organisms with females and males, i.e. organisms producing large and small gametes, respectively. However, those organisms descend from isogamous ancestors, i.e. organisms that did not produce different gametes, and all eukaryotic supergroups still contain isogamous groups. Lehtonen *et al.* [5] analyse the evolutionary causes and consequences of the transition from isogamy to anisogamy. They argue that lineages that evolved anisogamy,

thus carrying the highest costs of sex, end up being constrained, making the reversal to asexuality unlikely.

As Stelzer & Lehtonen [15] and Nieuwenhuis & James [9] make clear, in many organisms sex is facultative, or even condition dependent [19]. This is an important notion. For example, most calculations of the cost of sex are based on 'standard' organisms where reproduction and sex are obligatorily coupled, and where there are males. If sex is facultative, the timing of sex can be such that the so-called opportunity costs, i.e. the costs relative to the alternative of asexual reproduction, are minimal, which changes the whole calculation of the cost of sex [20]. However, Stelzer & Lehtonen's [15] analysis indicates that purely asexual or sexual strategies usually are superior to facultative strategies. Therefore, a highly specific mechanism (such as diapause linked to sex) is required to stabilize facultative sex.

One of the secondary consequences of bringing the genomes of two individuals together in a single zygote is opening the door to exploitation. Schwander & Oldroyd [14] discuss an extreme example of this, androgenesis, where males exploit the female gamete and eliminate the female's genome to transmit their own genome only. Haig [8] addresses potential conflicts between male and female haploid 'interests' in mosses and ferns, which may be played out both before and after gamete fusion, and trade-offs between sexual and asexual fertility. In mosses, a haploid gametophyte produces eggs that get fertilized by sperm produced by the same or a different gametophyte to produce a diploid sporophyte. After fertilization, the gametophyte 'mother' supports that diploid sporophyte, which grows on top of her. In the moss life cycle,

the haploid 'mother' thus invests before fertilization and supports an unrelated haploid genome of her mating partner after fertilization. This provides an interesting parallel to the lifecycle of mushroom-forming fungi. Vreeburg *et al.* [10] discuss how, in mushroom-forming fungi, the separation in time between gamete fusion and genome amalgamation increases the risk of genomic conflict. They show that the long-term 'living apart together' of nuclei in those organisms can lead to competition among the two nuclei for 'extramarital affairs', and show that this can favour traits that can reduce organismal fitness.

Another secondary consequence of sex is sexual selection via selection for mating success. Most of the models explaining sexual selection are based on animals with separate sexes and conspicuous secondary sexual characteristics that attract females (the peacock's tail), or aim to outcompete conspecific males (horns, antlers). However, Beekman *et al.* [11] take a detailed look at sexual selection when it is applied much more generally, to include simultaneous hermaphroditic organisms, and organisms that do not even come in direct contact, such as spermcasters, broadcast spawners, plants and fungi.

We hope you will enjoy the eclectic collection of contributions to this special issue. Your view on sex is bound to change. If your concept of what is 'normal' with respect to sex is shattered after having read through the papers, we will have achieved our goal. Sex will never be the same. Enter the wonderful and intriguing world of *Weird Sex*.

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Authors' profile



Duur Aanan is an associate professor in Evolutionary Biology at Wageningen University, The Netherlands. He specializes on the origin and evolution of cooperation, and conflicts between the levels of selection. The levels he addresses range from interspecific cooperation between fungus-growing termites and their symbiotic fungi to cooperation between genomes within cells. After finishing his PhD on speciation of fungi at Wageningen University in 1999, he became a postdoc and later assistant professor at the University of Copenhagen and returned to Wageningen in 2006. Duur Aanan uses fungi as his main experimental model system. Fungal 'individuals' can fuse and form chimeras, can be used in evolution experiments and are important mutualistic partners of other species, characteristics that make them excellent model systems for the evolution of conflict and cooperation.



Madeleine Beekman is a professor in Behavioural Ecology at the University of Sydney. She has always been fascinated by insects in general and social insects in particular. She did her PhD at the University of Amsterdam addressing life-history questions in bumblebees. After finishing her PhD in 1998, she moved to the University of Sheffield, where she worked both on honeybees and ants, a 'tradition' she maintained after her move to the University of Sydney in 2001. More recently, she started to incorporate other model organisms, some of which are rather unconventional, such as an acellular slime mould. The slime mould is an excellent model organism to address a range of evolutionary questions, such as the evolution and consequences of uniparental inheritance but also the origin of decision making.



Hanna Kokko completed her PhD in 1997 at Helsinki University. She is now a Professor of Evolutionary Ecology at the University of Zurich, where she landed in 2014 after holding an Australian Laureate Fellowship at the Australian National University. She has a longstanding interest in the mathematical logic that underpins biology—having published a textbook *Modelling for field biologists and other interesting people*—and displays particular curiosity towards the evolution of reproductive strategies. She is an invited member of two academies of science (in Finland and in Australia) and the recipient of the 2010 Per Brinck Oikos award, a prize awarded annually for a world-leading ecologist.

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